SOME HABITAT RESPONSES OF THE LARGE WATER-STRIDER, GERRIS REMIGIS SAY. II

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IV. DESCRIPTION OF AND EXPERIMENTS IN CONNECTION WITH BROOK HABITAT AT SYRACUSE

1. Description of Habitat.—Some further experimental work, much like that which previously has been considered, was done near a small, rapid stream (Figs. 4, 5), approximately 4.5 miles southwest of Syracuse, New York, in the late summer of 1918. The stream flows in an easterly direction, into Onondaga Creek, its source being a spring in the hills, forming the western side of Onondaga Valley. Water-striders, *Gerris remigis,* are common in certain situations on the surface of this brook (Figs. 4, 5). The water in the stream is clear, and its channel contains silt, gravel, small and large rocks. There is little rooted aquatic vegetation growing along the greater part of its course. At certain places the current is quite rapid, but even at those points where it is swiftest, there are small areas of quieter water, protected by rocks, or points of land jutting out into the stream. In such situations (Fig. 4) are found water-striders, singly and in small groups of two, three, or four individuals. Occasionally there is a short reach of quieter water, sometimes protected by trees (Fig. 5), on the surface of which water-striders are found in small numbers. Near the headwaters there is a large pool, formed mainly by an artificial dam, and this is separated into two parts by the decaying trunk of a large fallen tree. *Chara* grows rankly and in great mats in the pool. On its surface water-striders live in large numbers (Fig.

6). At this place, I have captured gerrids by the hundreds. I have examined this pool and the immediate vicinity for two successive seasons and I am convinced that they breed here from year to year. They undoubtedly hibernate, in large numbers, along the shores of

Fig. 4. Detail of small, rapid brook near Syracuse, showing spring conditions (May). Arrow indicates direction of current. *a*, areas of quieter water, formed by points of land, jutting out into the stream. Water-striders, *Gerris remigis*, are found, in small numbers, in such situations. (Original. Whitney.)

this pool. In fact I have found a few of them hibernating in interstices where the shore slightly overhangs the water, and also among dead leaves and other vegetation at points from a few inches to three yards away from the pool (Fig. 6).

2. *Methods.*—The experiments were performed on the shore of the pool, which is a large one for such a small brook. The dimensions of this body of water are approximately $55 \times 17 \times 2.5$ feet. The shore, where the experimental work was done, is flat and its surface is only a few inches higher than that of the water (Fig. 6). Back of this flat area, a little more than three yards away from the pool, there is a hill with a moderate slope. Only those experiments will be considered here that were carried far enough to evince fairly definite results. The water-striders used in these experiments were taken directly from the surface of the pool. Different individuals were used in each experiment. All these experi-

ments were carried on at Syracuse in the afternoon, at which time there was considerable reflection of the rays of the sun from the surface of the water.

3. Responses When Facing Away from Pool.—The first set of experiments deals with gerrids that were placed on the ground one yard away from the margin of the

FIG. 5. Detail of small, rapid brook near Syracuse, showing spring conditions (May). *a*, reach of quieter water, protected by trees; water-striders, *Gerris remigis*, are found in small numbers in such situations. (Original. Whitney.)

water. The heads of the gerrids were pointed directly away from the pool. In general, the responses of the water-striders, in those experiments performed under like conditions, showed much similarity. Therefore, I give a condensed account of several typical experiments.

Experiment VI.—The water-strider is placed on the ground. It immediately turns and faces the pool, and at once begins to jump toward the water. While the gerrid does not turn away from the pool, it jumps toward it slowly. Thirty seconds after being placed on the ground, the insect is back on the surface of the pool.

Experiment VII.—After being placed on the ground, the gerrid turns toward the pool, and jumps in the direction of the water for a distance of one foot. During one of the jumps, the body is so oriented that the head is turned away from the pool. The water-strider continues to jump, but is now moving away from the water. It proceeds in the same direction until it reaches a point four yards away from the pool

and part way up the side of the slope. This gerrid is observed for ten minutes and is still jumping away from the water.

Experiment VIII.—This water-strider jumps away from the water for a distance of five inches. It now turns directly to the right, which position places the long axis of the body parallel with the margin of the pool. I am not sure whether this turn is due to the body striking against some object during a jump, or whether the water-strider makes the turn as a result of some other stimulus. The gerrid jumps and walks parallel with the margin of the pool for a distance of two yards. In a few seconds it turns a little more to the right, so that it is now

FIG. 6. Detail of large pool at headwaters of small, rapid brook near Syracuse, showing spring conditions (May). *Chara* grows in great abundance in this pool. *a*, surface of pool on which water-striders, *Gerris remigis*, are found in large numbers; *b*, vegetation and dead leaves among which water-striders hibernate; *c*, overhanging shore of pool in interstices of which water-striders hibernate; *d*, shore of pool where experiments were performed; *e*, artificial dam built of concrete. (Original. Whitney.)

jumping obliquely toward the water. The insect continues to move in the same direction until it reaches the pool. This gerrid is back on the surface-film of the water in twenty-five seconds after the experiment began.

Experiment IX.—The water-strider is placed on the ground and it immediately turns to the left, thus placing the long axis of the body parallel with the margin of the pool. The creature jumps straight ahead for a few inches, and then turns obliquely toward the water. It moves along rapidly and soon attains the surface-film. This gerrid reaches the pool in twenty-five seconds from the time it first was placed on the ground.

Experiment X.—This water-strider at once turns in such a manner

that the longitudinal axis of the body is placed parallel with the margin of the pool. The gerrid walks for five inches in a path parallel with the shore of the pool. It now turns so that its head points away from the water, and jumps in that direction for two feet. The insect again turns, this time the head being directed toward the water, but it walks in that direction for two inches only. It turns to the left, thus again placing the body parallel with the margin of the pool. The gerrid jumps straight ahead for four feet, and again turns directly toward the water, jumping rapidly along a practically straight path until it reaches the pool. The creature is back again on the surface of the pool in forty seconds after the experiment began. This water-strider was active from the time it was placed on the ground until it reached the water.

Experiment XI.—The gerrid walks away from the water for a distance of two inches. It then turns to the left and jumps along a path parallel with the margin of the water for four inches. The insect now makes a turn of ninety degrees, so that its head is directed toward the pool, and jumps rapidly to the water. In fourteen seconds after being placed on the ground, the gerrid is striding back and forth on the surface of the pool.

In these experiments I have condensed the statements in such a manner as to give prominence to the factors of time and direction. With reference to these particular elements, the experiments are typical of many others recorded in my field notes. It is evident that a large majority of the gerrids get back safely to the water, only one out of the six failing to do so. This was the individual used in Experiment VII. A large number of experiments furnish similar results. Although there were a number of random and trial movements, the water-striders returned to the pool with a fair degree of promptness. The total amount of time consumed by all the gerrids was 12 minutes and 14 seconds. The average time taken to reach the water was 2 minutes and $2\frac{1}{3}$ seconds. Omitting Experiment VII, the total amount of time necessary for all the gerrids to get back into the pool was 2 minutes and 14 seconds. With this experiment omitted, the average time consumed in reaching the water was $26\frac{4}{5}$ seconds. These results are indicated in Table I. The results of two other sets of experiments are indicated in Table II and Table III. Attention is directed to the similarity in the records of the three series of experiments as expressed in the tables.

TABLE I

TIME CONSUMED BY WATER-STRIDERS IN REACHING WATER FROM DISTANCE OF 1 YARD

Experiments				
Heads Directed Away from Water	Time Consumed		Responses	
Number of Experiment	Minutes	Seconds	Successes	Failures
VI	0	30	+	..
VII	10	0	..	—
VIII	0	25	+	..
IX	0	25	+	..
X	0	40	+	..
XI	0	14	+	..
Totals 6	12	14	5	1
Averages	2	$2\frac{1}{3}$	$0\frac{5}{6}$	$0\frac{1}{6}$
Totals, omitting experiment VII	2	14	5	0
Averages, omitting experiment VII	0	$26\frac{4}{5}$	1	0

TABLE II

TIME CONSUMED BY WATER-STRIDERS IN REACHING WATER FROM DISTANCE OF 1 YARD

Experiments				
Heads Directed Away from Water	Time Consumed		Responses	
Number of Experiment	Minutes	Seconds	Successes	Failures
XVIII	0	18	+	..
XIX	0	20	+	..
XX	0	25	+	..
XXI	0	28	+	..
XXII	0	35	+	..
XXIII	1	0	+	..
Totals 6	3	6	6	..
Averages	0	31	1	..

4. *Responses When Facing Pool.*—A condensed statement will be given now of experiments in which the heads of the water-striders were turned toward the pool. As before, the gerrids were placed one yard away from the water. Special attention again was directed to the factors of time and direction.

Experiment XXX.—The water-strider jumps three inches directly toward the water. It then turns to the right, jumping parallel with the margin of the pool for one foot. The gerrid again turns slightly to the right, being now in a position oblique to the pool, and continues jumping away from the water for two feet. The insect turns to the left, so that its head points obliquely toward the pool, and jumps in a

TABLE III

TIME CONSUMED BY WATER-STRIDERS IN REACHING WATER FROM DISTANCE OF 1 YARD

Experiments				
Heads Directed Away from Water	Time Consumed		Responses	
Number of Experiment	Minutes	Seconds	Successes	Failures
XXIV	0	20	+	..
XXV	0	30	+	..
XXVI	15	25	..	—
XXVII	0	32	+	..
XXVIII	0	50	+	..
XXIX	0	18	+	..
Totals 6	17	55	5	1
Averages	2	$55\frac{5}{12}$	$0\frac{5}{6}$	$0\frac{1}{6}$
Totals, omitting experiment XXVI	2	30	5	0
Averages, omitting experiment XXVI	0	30	1	0

straight path until it reaches the water. This water-strider consumed twenty-five seconds in making the journey to the pool.

Experiment XXXI.—This gerrid jumps in a zigzag course toward the water, arriving on the surface-film of the pool in ten seconds from the time it was first placed on the ground.

Experiment XXXII.—The water-strider moves toward the pool, jumping in a direction slightly oblique to its margin and gaining the water-film in twelve seconds.

Experiment XXXIII.—The path taken at first, by this water-strider, is toward the pool, but after jumping for a distance of four inches in that direction, it turns obliquely to the right, still jumping toward the water. The gerrid is back on the surface of the pool in eleven seconds from the time it was placed on the ground.

Experiment XXXIV.—This hemipteron takes a position so that the body is slightly oblique with reference to the margin of the pool. The gerrid jumps along a straight path toward the water for two feet. It now turns so that the long axis of the body is parallel with the margin of the pool. It jumps straight ahead for one yard, when it turns toward the water, arriving at the pool in ninety seconds.

Experiment XXXV.—This gerrid turns to the right, as soon as it is placed on the ground, and jumps for a distance of two feet in a direction parallel with the margin of the pool. It then makes a turn of ninety degrees to the left, thus pointing its head directly toward the water. The creature jumps in this direction until it reaches the pool, twelve seconds after the experiment began.

The results evinced in these experiments are typical of the results obtained in many others not recorded here, except a few which are indicated by tables. It is noticed that the water-striders reached the pool much

more promptly than was the case when they were placed on the ground with their heads directed away from the water. All the gerrids reached the water—as was generally the case in many other experiments of a similar character—with but a limited number of random movements. The only prominent exception to this was the gerrid used in Experiment XXXIV. Usually, there were one or two individuals that displayed this lack of promptness. All the gerrids employed in the six experiments consumed a total amount of time of 2 minutes and 40 seconds. The average amount of time necessary to return to the pool was 26⅔ seconds. If Experiment XXXIV should be omitted, it is evident that the total amount of time consumed by five water-striders in reaching the pool was 1 minute and 10 seconds. The omission of this experiment reduces the average time, consumed in reaching the water, to fourteen seconds. These results

TABLE IV

TIME CONSUMED BY WATER-STRIDERS IN REACHING WATER FROM DISTANCE OF 1 YARD

Experiments				
Heads Directed Toward Water	Time Consumed		Responses	
Number of Experiment	Minutes	Seconds	Successes	Failures
XXX	0	25	+	..
XXXI	0	10	+	..
XXXII	0	12	+	..
XXXIII	0	11	+	..
XXXIV	0	90	+	..
XXXV	0	12	+	..
Totals 6	2	40	6	..
Averages	0	26⅔	1	..
Totals, omitting experiment XXXIV	1	10	5	..
Averages, omitting experiment XXXIV	0	14	1	..

are shown in Table IV. The results of other experiments of a similar character are indicated in Table V and Table VI.

5. *Responses When Parallel With Pool.*—Some experiments were performed with water-striders having the long axis of the body parallel with the margin of the pool. In all other respects, the conditions were similar

TABLE V

TIME CONSUMED BY WATER-STRIDERS IN REACHING WATER FROM DISTANCE OF 1 YARD

Experiments				
Heads Directed Toward Water	Time Consumed		Responses	
Number of Experiment	Minutes	Seconds	Successes	Failures
XXXVI	0	20	+	..
XXXVII	0	15	+	..
XXXVIII	0	17	+	..
XXXIX	0	22	+	..
XL	0	20	+	..
XLI	0	18	+	..
Totals 6	1	52	6	..
Averages	0	$18\frac{2}{3}$	1	..

TABLE VI

TIME CONSUMED BY WATER-STRIDERS IN REACHING WATER FROM DISTANCE OF 1 YARD

Experiments				
Heads Directed Toward Water	Time Consumed		Responses	
Number of Experiment	Minutes	Seconds	Successes	Failures
LI	0	13	+	..
LII	0	17	+	..
LIII	0	12	+	..
LIV	0	14	+	..
LV	0	12	+	..
LVI	0	16	+	..
Totals 6	1	24	6	..
Averages	0	14	1	..

to those when the heads were directed toward and when they were directed away from the pool. The results were much like those evinced in Table II, except that the time consumed in reaching the water was slightly greater in the majority of cases. There was a little less promptness, perhaps, in moving toward the water and a greater number of trial directions. Occasionally a gerrid did not reach the pool at all.

6. Responses When Not Oriented with Reference to Pool.—A number of other simple experiments were carried out near the large pool in the brook previously mentioned (Fig. 6). In these the water-striders were not oriented with reference to the position of the pool at the beginning of each experiment. Forty gerrids just

captured from the surface-film were put into a small wooden box. This was taken to the place where the other experiments were performed (Fig. 6). It was then inverted and all the water-striders carefully shaken out on to the ground one yard away from the water. It was of course impossible to watch in detail every gerrid, but it was possible to observe how many of the hemipterons reached the water. The majority of them were back on the surface-film within fifteen seconds after being placed on the ground. All but two individuals had reached the water within thirty-five seconds after the experiment began. At the end of one minute of time all the gerrids were on the surface of the pool. Sometimes a water-strider was not successful in reaching the pool. These statements are fairly typical of the results of many other similar experiments.

A series of experiments of a similar character was undertaken in which the gerrids were placed on the ground three yards away from the pool. As in the experiments one yard away from the water, the hemipterons found the surface of the pool with reasonable promptness and directness. The greater number reached the water within forty seconds from the time that they touched the surface of the ground. In the majority of these experiments, all the water-striders were back on the surface of the pool, 2 minutes and 5 seconds later. In each of two different trials, out of a total of six, there were two gerrids that jumped away from the pool and had not reached the water at the time my observations were discontinued. I believe that vision was the chief factor employed in directing the gerrids to the water in the experiments when forty individuals were used at each trial.

I have not yet observed the results of placing the water-striders on the ground in large numbers farther away from the pool than three yards. Nor have I made any trials, either in the vicinity of Urbana or Syracuse, with the gerrids for a greater distance from the water than four yards.

V. Discussion of Observations at White Heath

1. Initial Locomotor Responses.—It is an interesting fact that, just previous to the drying up of the pool, in which the water-striders were living, there were no responses on the part of the gerrids which indicated any attempt to escape from the unfavorable surroundings. Not until the water had disappeared entirely was there any tendency to leave the place. Soon after it became dry the water-striders began to move away from the site of the former pool. What the immediate stimulus was, it is difficult to say. A change in the physiological condition of the body, which might have been induced by the drying up of the pool, would be sufficient to account for the locomotor responses. Whatever the stimulus was, the gerrids began to walk and jump away in different directions. But as Jennings (1906, pp. 284, 285) has pointed out:

> Often . . . movement in a certain direction is due only to the release of inhibition. The organism moves in the given direction because it is moving from internal impulse, and because movement in this direction is not prevented. This possibility must be considered in all cases.

Therefore, it is not always necessary to assume that movement is due to some very recent external stimulation. Whatever the explanation may be, the water-striders moved off in the direction in which their heads were pointed. They continued along the same line of progress until they arrived at some obstacle in their pathway. Such an obstacle might be a lump of dried mud, a stone, or a piece of driftwood. Then they usually turned to the right or left, as the case might be, thus being deflected from their former direction of movement. They continued along the new path until they were deflected again, in a new direction.

2. Rôle of Trial and Error.—Such responses as previously have been described occurred again and again. The various objects in the path of the water-striders served as stimuli to turn the gerrids aside and swerve them in another direction. First they tried one line of

progression and then they tried another. As Holmes (1916, pp. 157, 158) has said:

> Where there is "error," the organism tries again, and keeps on doing so until it attains ultimate success.

This statement does not mean that all achieve success, nor does it necessarily mean that the organism possesses any conscious appreciation of means to an end. Certainly, I do not consider that water-striders have such an appreciation. Frequently, on coming in contact with such obstacles, as have been mentioned, the gerrids came to rest with the side or sides of the body closely applied to the object. This was due to their thigmotactic proclivities. They remained in such positions for varying lengths of time and then moved forward again, but usually the direction of progression was changed. Occasionally, they remained motionless in such situations until the time set for me to discontinue my field observations for that particular day. Sometimes individuals crawled under lumps of dried mud, under pieces of driftwood, or among dead leaves. On a few occasions, a few gerrids jumped into large cracks in the baked mud of the stream bed. Water-striders getting into such places, occasionally remained there, but I never have been able to find them the day following the observation.

It already has been stated that some of the gerrids reached the larger pool of water some distance downstream, and attention also has been directed to the fact that on several other occasions, when water-striders had been trapped in stream pools, some of their number were successful in reaching other bodies of water in the immediate vicinity. I have not observed that gerrids ever were succesful in finding another body of water that was situated farther away than fourteen yards. In none of these cases that have come under my observation, have I been able to see that there was any definite response, on the part of the gerrids, to another body of water *per se*. In many instances, the locomotor movements of the water-striders, in so far as their final goal was concerned, have

proved to be lacking in definiteness, precision, and in direction of response. Their locomotor movements were very awkward and they stumbled along the route in a very blundering fashion. Their method, if it can be called such, of reaching the water seemed to be entirely one of chance. They might blunder on to a pool of water in the vicinity or they might not. They frequently took the wrong direction and made many mistakes. A better way, perhaps, to express my thought, is to state that these gerrids pass from the site of a former pool to another body of water by a blundering method of trial and error. As Holmes (1916, p. 158) well has said:

> The method is round about and expensive, but it is better than nothing. It is Nature's way of blundering into success.

It is not improbable that the method of trial and error forms a large part of the habitat responses of arthropods. It is certainly true that a number of writers have been impressed with the prevalence of behavior of such a character among the members of this group. Among others, this is evident from the work of Bohn (1903) in connection with hermit crabs. Holmes (1905, p. 106) in describing the behavior of the blow-fly larva, with reference to light, makes the following statement:

> It may be said to be a form of the trial and error method minus the element of learning by experience.

Writing of the trial and error method in the conduct of lower animals, Holmes (1905, p. 108) states that:

> The lives of most insects, crustaceans, . . . and hosts of lower invertebrate forms, . . . show an amount of busy exploration that in many cases far exceeds that made by any higher animal.

In this connection the following general statements are of great interest, as they show the importance that is now attached to such a method of conduct among invertebrates: Holmes (1905, pp. 107, 108) points out that:

> The rôle played by the trial and error method in the behavior of the lower organisms has, as yet, elicited but little comment, owing probably to the fact that attention has been centered more upon other features of their behavior. It may have been considered by some investigators as

too obvious for remark since any one who attentively observes the conduct of almost any of the lower animals for ten minutes can scarcely fail to see the method exemplified.

Jennings (1906, pp. 246, 247), also, directs attention to this form of behavior in the following words:

In most if not all other invertebrates there occur many "trial movements" similar to those already described. In many recent accounts of the behavior of other invertebrates little mention, it is true, will be found of such movements. This is apparently because attention has been directed by current theories to other features of the behavior, and the trial movements have been considered of no consequence. Often an attentive reading of papers on "tropisms," etc., will reveal parenthetical mention of various "disordered" movements, turnings to one side and the other, and other irregularities, which disturb the even tenor of the "tropism," and are looked upon for some reason as without significance and not requiring explanation. Further, one often finds in such papers accounts of movements which are clearly of the "trial" character, yet are not recognized as such by the author, on the watch only for "tropisms." In the earlier literature of animal behavior, before the prevalence of the recent hard-and-fast theories, one finds the trial movements fully recognized and described in detail. . . .

Unprejudiced observation of most invertebrates will show that they perform many movements which have no fixed relation to sources of external stimuli, but which do serve to test the surroundings and thus to guide the animal. . . . As Holmes (1905) has recently pointed out, in a most excellent paper, this is really a matter of common observation on all sorts of animals. The fact that such movements are not emphasized by writers on animal behavior is evidently due to their being considered without significance.

In a number of recent papers the importance of trial movements in behavior has been more explicitly recognized. . . .

I have made a statement about a final goal, but I do not intend to convey the idea, in any way, that these insects are endowed with even the smallest amount of prevision, nor do I wish to be understood as assuming that because of certain perception, on the part of the water-striders, of the exigencies of the case, they therefore responded with a special form of behavior suitable to meet the difficulties of the situation. But, on the other hand, I wish to present the thought that these gerrids, in moving away from their former haunts, may or may not come upon another body of water, if there is one in the vicinity, and that this hap-

pens not because of any direct or definite response or responses to the body of water *per se,* but rather is due more to the fact that many of their locomotor responses are spontaneous ones, modified frequently as to direction and speed, mainly, by contact stimulus, many of these movements probably being due not to some very recent stimulus or stimuli which have any direct relation to the body of water, but that they, more probably, are due, as Jennings (1906, p. 285) suggests,

> to the simple outflow of the stored-up energy of the organism through the channels provided by its structure.

3. Rôle of Moisture.—Undoubtedly it is true that water-striders, *Gerris remigis,* are sensitive and responsive to moisture. The fact that the greater portion of their lives is passed on the surface-film of brooks and streams would seem to be sufficiently indicative of this. Then, also, the ability to find their way back to the stream in the spring, having left it in the fall, frequently from distances of three and four yards, and sometimes from greater distances, after passing several months in hibernation, is further indication that they are sensitive to some stimulus or stimuli, the response to which results in bringing them back to the water.

That the migration of these gerrids from the site of a former pool to another body of water is mainly an expression of hydrotropism, according to the manner in which that form of response is usually interpreted, I believe to be extremely doubtful. However, it is not my intention to assert that moisture does not play an important rôle in the economy of these water-striders. But I do not believe that the movements of the gerrids in the dry bed of the brook afford any definite indication that they are direct responses to moisture. It is very improbable that, during severe droughts and high temperatures, moisture, diffusing through the atmosphere, from such comparatively small bodies of water (dimensions 3 yds. $\times$ 2 yds. $\times$ 5 in. and in several instances smaller than this) as already have been indicated, impinged on the bodies of

the hemipterons in any manner that would be effective in producing definite responses to the source of this moisture, as for example positive responses, resulting in the water-striders wandering toward the pool. This is the more improbable when it is recalled that the gerrids were ten yards away from the water, and in other instances, not recorded in detail in this paper, they were even farther away than this, eleven, twelve and fourteen yards distant. I also have observed their responses in the dry bed of a stream, when there were pools of water at a less distance than ten yards apart.

In this connection it may be of interest to quote a statement from Weiss (1914, p. 33):

> Wingless forms of *Gerris marginatus,* which is quite common throughout New Jersey, when removed from a pond containing some three thousand square feet of water and liberated at distances of one, two, three, four, five, six, seven, eight, and nine yards from the water, immediately made their way back to the water without hesitancy. Of course their movements, which consisted of a series of jumps, were more or less clumsy, but all started in the right direction even though purposely headed the wrong way.
>
> When liberated at a distance of ten yards, they had some slight trouble in getting their bearings, but after making several false starts, finally wound up by going in the direction of the water. At a distance of fifteen yards, a longer time and more moving around were required before the right direction was located. At thirty and forty yards away, they seemed to lose their bearings completely and moved aimlessly about in all directions. Even at the end of an hour they were no nearer the water.

The observations of Weiss were of responses of water-striders under experimental conditions and not observations of their responses under the natural conditions of their own environment undisturbed by any extraneous stimulus, as was the case of my observations. However, it is pertinent to direct attention to certain facts in connection with his experiments. It is evident that the responses of *Gerris marginatus,* especially those individuals that were placed on the ground seven, eight, and nine yards away from the water, differ from those of *Gerris remigis.* Members of this species do not make their way to water, from such distances, with the promptness and

definiteness recorded in the experiments of Weiss with individuals of *Gerris marginatus*. I infer from the little description recorded, that the responses of individuals of the same species, when placed on the ground ten yards away from the water, were more of the character of those of *Gerris remigis* at such a distance from a pool of water. While I have not observed gerrids of this species make their way to a body of water quite so far away as fifteen yards distant, as did Weiss in some of his experiments with *Gerris marginatus,* yet I am not prepared to state that they can not do so. However, if they are able to find water at such a distance, I believe that the achievement is one purely of chance, or the result of a blundering sort of trial and error. On one occasion, I observed individuals of *Gerris remigis* leave the site of a former pool in the bed of a stream and although I watched them for an entire afternoon, only one, out of a group of thirty, had reached an isolated pool fourteen yards distant, when I discontinued my observations at dusk. On another occasion, six water-striders only, out of a group of forty individuals, were successful in finding a body of water fourteen yards from the site of the pool in which they formerly had lived. I would expect, from my own observations of *Gerris remigis,* the responses of apterous *Gerris marginatus,* at distances of thirty and forty yards, to be much as described by Weiss, although I have recorded no observations of the responses of gerrids at such distances from water.

I believe that alate individuals of *Gerris marginatus,* during migration by flight, find bodies of water mainly through the sense of vision, as is probably true in the case of many different species of aquatic Hemiptera, a subject to which Kirkaldy (1899, p. 110) and other writers have directed attention. Recent work on phototaxis—(Holmes, 1905a), (Holmes, 1907, pp. 160, 161), (Cole, 1907, pp. 382–388), (Essenberg, 1915, p. 400), and (Riley, MS.)—has demonstrated that many species of aquatic bugs respond positively to light. *Benacus* and *Belostoma* respond to light during migration. In the fall of 1908, at

Mankato, Minnesota, a few hundred yards from a large swamp, near the confines of the city, I observed them for several nights, as they flew in great swarms, around the globes of the street arc lights. On the ground, within a radius of thirty to fifty feet of certain of the lights, were thousands of these aquatic bugs, both alive and dead. On several occasions, it was possible, in thirty minutes of time, to fill a half bushel measure with the insects. In the fall of 1915, at Milwaukee, Wisconsin, in the vicinity of Lake Park, between the Milwaukee River and the west shore of Lake Michigan, I observed several occurrences similar to those just described. In these instances, the aquatic bugs were not present in quite such large numbers as in the former cases. The point of importance here is, of course, the fact that members of the two groups, *Benacus* and *Belostoma,* respond positively to light during migration. Comstock and Comstock (1895, p. 132) refer to somewhat similar responses. All these facts add still more emphasis to the probability that alate gerrids, when migrating, locate streams and standing water by means of vision. It should be recalled that such bodies of water are effective reflecting surfaces. However, it is quite possible that both alate and apterous individuals of *Gerris marginatus* are responsive to moisture at greater distances than is the case with apterous members of *Gerris remigis.* If this should prove to be the case, it would be of assistance to the gerrids in finding bodies of water. Further, it must be recalled that the pond to which Weiss directs attention covered an area of 3,000 square feet, while the pools of water to which I refer were very small in size.

It is probably true that many arthropods respond readily to moisture. But there is not a great deal of experimental evidence recorded in the literature, treating of the behavior of members of the group, that presents definite information bearing on the particular phase of the subject under discussion. The experimental work that proved to be most nearly related to the form of be-

havior under consideration was found in a paper by Drzewina (1908) on the hydrotropism of crabs, *Carcinus mænas*. Because of the character of this work, I shall refer to it and quote from it at some length. This writer makes a careful analysis of the responses of these crustaceans to the sea. She noticed that when one of the crabs was placed on the beach that it oriented itself and moved toward the sea, even at a distance of 100 meters. Her statement (1908, pp. 1009–1010) follows:

Parmi les réactions du *Carcinus maenas* que j'ai eu l'occasion d'étudier pendant mon séjour au laboratoire maritime de Tatihou et à la station biologique d'Arcachon, une des plus frappantes est l'orientation du Crabe dans son habitat naturel. C'est un fait d'observation banal qu'un *Carcinus* déposé sur la plage se dirige aussitôt du côté de la mer, celle-ci pouvant être distante de plus de 100 mètres. Il m'a paru intéressant de déterminer les facteurs qui influencent cette orientation particulière.

Her observations seem to prove that both orientation to and direction of movement toward the sea were not due to responses to light, to the sight of the sea, to the wind, or to gravity, but on the other hand were due to the moisture given off by the sea. Observations were made every day for more than a month, at different times of the day, both in bright sunlight and also in cloudy weather. These facts are brought out in the following quotation (1908, p. 1010):

J'ai pu montrer que ni la lumière, ni la "vue" de la mer, ni la direction du vent n'interviennent dans ce phénomène. J'ai fait des expériences, et j'ai obtenu des résultats identiques, aux différentes heures de la matinée et de l'après-midi, avec un soleil vif ou sous un ceil couvert; les *Carcinus* dont les yeux ont été noircis ou sectionnés se comportaient à ce point de vue comme des Crabes normaux. Comme mes expériences ont été faites tous les jours pendant plus d'un mois, j'ai eu le vent venant soit de la terre, soit de la mer, soufflant dans diverses directions, vent très fort, ou faible, ou nul, ce qui ne modifiait pas sensiblement le sens de l'orientation des animaux; bien entendu, quand se vent était fort, il pouvait accélérer ou arrêter les mouvements des Crabes.

En ce qui concerne l'inclinaison de la plage, celle-ci exerce bien une influence sur les mouvements du *Carcinus*, qui, souvent, se laisse entraîner par elle et suit, dans la descente, la ligne de la plus grande pente; mais ce n'est pas elle qui le guide dans son orientation par rap-

port à la mer. J'ai pu en effet montrer, en faisant marcher des Crabes sur des pentes creusées artificiellement et diversement inclinées, que ces animaux peuvent tout aussi bien descendre que monter les pentes dans leur "fuite" vers la mer.

Après avoir éliminé successivement divers facteurs, je me suis arrêtée à cette hypothèse: les Crabes se dirigent du côté de la mer attirés par l'humidité dégagée par celle-ci; il y aurait *hydrotropisme.*

Drzewina noticed the character of the behavior of the crabs after a heavy rain. The peculiarity of this behavior seemed to present additional evidence that the movements of the crustaceans, previously mentioned were responses to the moisture from the sea. At such a time the ground was very moist. Therefore there was no longer a sharp contrast between the land and the sea, with respect to the amount of water vapor given off by each. The crabs did not go directly toward the sea; but some of them moved obliquely to the right and to the left; others followed a zigzag course, parallel to the sea; while still others climbed a slope and proceeded in a direction opposite from the sea. I will record these very interesting observations in her own words (1908, p. 1010):

Plusieurs faits que j'ai observés viennent á l'appui de cette hypothèse. Après une pluie abondante, le sol étant humide, quand on dépose les Crabes sur da pente sableuse, ils ne se dirigent pas directement vers la mer, comme ils le font d'habitude, mais ils vont d'une façon quelconque: les uns obliquent à droite ou à gauche, d'autres vont en zigzaguant parallèlement à la mer, d'autres enfin remontent la pente, dans le sens opposé à la mer. Il est évident que dans le cas présent, comme il n'y a plus de contraste assez net entre la mer et la terre, celle-ci dégageant également de la vapeur d'eau, l'orientation des Crabes se fait d'une façon de la quelconque.

This observer found that, when a crab was placed in front of a kind of dyke, which at low tide separated two bodies of water, the animal did not respond by moving toward either body of water, but, instead, it took an intermediate direction, and walked toward the dyke. She recorded these facts as follows (1908, pp. 1010, 1011):

Voici un autre fait intéressant au point de vue de l'hydrotropisme: Je dépose un Crabe en face d'une sorte de digue qui, à mer basse, sépare deux masses d'eau s'éntendant à droite et à gauche. Le Crabe est attiré

à la fois par l'une et par l'autre; il prend une direction intermediaire et va vers la digue au lieu d'aller vers une des bandes d'eau.

The responses of crabs living in shallow water differed from the responses of those living in deeper water. When the former were placed on the beach, they displayed a very definite hydrotropism, but the latter, under similar experimental conditions, evinced no such definiteness of response. Drzewina considered such responses to be adaptive in character. She seems to infer that the character of the behavior, already acquired, must be taken into consideration in the interpretation of their present responses. These observations are described by her as follows (1908, p. 1011):

Quand on prend le même Crabe dans divers habitats, on s'aperçoit que son orientation est adaptée aux conditions dans lesquelles il vit et qu'elle correspond aux habitudes qu'il a pu acquérir dans le cours de son développement. Les Crabes de hauts niveaux, ayant à subir de courtes périodes de submersion alternant avec les périodes d'émersion, c'est-à-dire de dessiccation relative, sont très sensibles aux contrastes de l'humidité et de la secheresse et, déposés sur la plage, manifestent un hydrotropisme très net. Mais les *Carcinus* des niveaux plus bas, pris sur fond vaseux se comportent autrement: déposés sur la plage, ils se dispersent dans toutes les directions, devient facilement, et, surtout, se terrent constamment; d'une manière générale ils sont lents, peu sensibles aux contrastes de l'ombre et de la lumière.

4. Rôle of Vision.—On the several occasions that I have observed the drying up of isolated stream pools, having on their surfaces trapped *Gerris remigis,* I have watched carefully in order to detect whether the sense of sight was the principal factor in aiding these aquatic bugs to find other bodies of water. The rôle played, directly, by vision, is probably not of immediate importance during their responses in this connection, except in those instances when the ground is flat and level and the gerrids are comparatively close to the water. There are various obstacles that modify the possibilities of such an explanation. If there are two or more bodies of water in the immediate vicinity, it has been observed that the gerrids are just as likely to move toward the farthest one, as they

are to move toward the nearest one. If vision were the main factor in assisting the hemipterons in finding pools of water, they would be expected to go to the nearest one first. Another fact against the idea of vision being the chief influence in guiding these insects to water is that the dry channels of the streams, where I have made my observations, frequently have very rough and uneven surfaces, with small boulders, stones, lumps of baked mud, pieces of driftwood, and clumps of dead leaves scattered along them. When the small size of these insects and the nearness of their eyes to the surface of the ground are both taken into consideration, it becomes very evident that the various objects that have been enumerated must obstruct the view of the water-striders in a very serious fashion. Then again, sometimes the nearest pool was around a bend in the stream, away from the gerrids, thus making it impossible to be seen by them at a distance.

With reference to the experiments of Weiss (1914, p. 33) it is probable that sight was an important factor in directing the gerrids to the water, especially over the shorter distances, one to six yards inclusive. On a bright, sunny day, it is evident that the glistening and reflective qualities of a body of water must be factors of importance in attracting these aquatic hemipterons. It must be recalled that the pond to which Weiss refers was a body of water extending over an area of 3,000 square feet in extent while the pools to which I have referred were proportionately insignificant in size. If there was a gradual slope to the shore of this pond and if the ground, where the experiments of Weiss were performed, had a smooth surface free of obstructions to the view, all this should be in favor of the idea that vision was the important factor in directing the water-striders back again to the pond. However, the local physical conditions are not described.

Certain experiments of Drzewina (1908) are, perhaps, worthy of mention in this general connection. This writer found, in her observations on the hydrotropism of crabs, that these animals responded positively, and with

considerable precision, to the moisture given off from the sea. However, in other experiments with crabs she considered that the past life of the crustaceans and the character of the behavior, already acquired, must be taken into consideration, in the interpretation of their present responses. Crabs, living in deep water, among rocks covered with algæ and beaten by the waves, when placed on the sand, in the vicinity of the sea, did not evince definite hydrotropic movements, but, on the other hand, their responses were of a very different character. The factor, in these responses, of importance to the present discussion is that of sight. Vision, apparently, played a prominent rôle in determining the direction of movement of the crabs. Drzewina (1908, p. 1011) has given a rather full statement concerning these facts:

Les *Carcinus* de la zone basse de *Fucus serratus,* pris à une pointe rocheuse (Gatteville), où ils vivent cramponnés parmi les rochers couverts d'algues et battus par les flots, se comportent encore autrement: lâches sur du sable, au voisinage de la mer, au lieu de descendre vers celle-ci, ils se dirigent immédiatement, en ligne droite, vers des rochers couverts d'algues, ces rochers pouvant etre sitúes a plusieurs mètres de distance latéralement à droite, à gauche, ou à la limite d'eau, ou même dans le sens opposé à la mer. Et ceci, quelle que soit la direction du vent et du soleil. Ces mêmes Crabes, déposés sur du sable clair, légèrement humide, où, par places, se trouvent disséminées des taches sombres de *Fucus,* se dirigent vers ces taches. Jamais je n'ai pu constater, avec ces Crabes, d'orientation directe par rapport à la mer, mais toujours une attraction très prononcée exercée soit par des rochers, soit par des touffes d'algues, par des surfaces d'ombre, en un mot.

Ces quelques faits montrent combien il est important, dans l'interprétation des réactions, de tenir compte du passé de l'animal et des "habitudes" que celui-ci a pu créer. Dans l'hydrotropisme du *Carcinus maenas,* l'intervention des habitudes est des plus manifestes.

(*To be concluded*)